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Evidence for widespread endemism among Antarctic micro-organisms

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Abstract

Understanding the enormous diversity of microbes, their multiple roles in the functioning of ecosystems, and their response to large-scale environmental and climatic changes, are at the forefront of the international research agenda. In Antarctica, where terrestrial and lacustrine environments are predominantly microbial realms, an active and growing community of microbial ecologists is probing this

diversity and its role in ecosystem processes. In a broader context, this work has the potential to make a significant contribution to the long-standing debate as to whether microbes are fundamentally different from macroorganisms in their biogeography. According to the ubiquity hypothesis, microbial community composition is not constrained by dispersal limitation and is solely the result of species sorting along environmental gradients. However, recent work on several, groups of microalgae is challenging this view. Global analyses using morphology-based diatom inventories have demonstrated that, in addition to environmental harshness, geographical isolation underlies the strong latitudinal gradients in local and regional diversity in the Southern hemisphere. Increasing evidence points to a strong regionalization of diatom floras in the Antarctic and sub-Antarctic regions, mirroring the biogeographical regions that have been recognized for macroorganisms. Likewise, the application of molecular-phylogenetic techniques to cultured and uncultured diversity revealed a high number of Antarctic endemics among cyanobacteria and green algae. Calibration of these phylogenies suggests that several clades have an ancient evolutionary history within the Antarctic continent, possibly dating back to 330 Ma. These findings are in line with the current view on the origin of Antarctic terrestrial metazoa, including springtails, chironomids and mites, with most evidence suggesting a long history of geographic isolation on a multi-million year, even pre-Gondwana break-up timescale.

Key words: microbial biogeography, isolation, dispersal ubiquity hypothesis, evolution

Introduction

Until recently, ice sheet models implied that as a result of successive Neogene and Late-Pleistocene glacial maxima, ice-free regions in Antarctica would have been overridden by ice for extended periods of time. Consequently, virtually all terrestrial life on the Antarctic continent would have been driven to extinction at glacial maxima and, as a consequence the present biodiversity would probably be derived from recent colonizations of regions that have become ice-free since the start of the Holocene. However, recent work on terrestrial invertebrates, including springtails, chironomids and mites, has challenged this view (reviewed in Convey et al. 2008, 2009). Fossil evidence, time-calibrated molecular phylogenies and population genetic studies, provide strong evidence that a significant fraction of the contemporary Antarctic terrestrial metazoa must have been continuously isolated on a multi-million year, even pre-Gondwana break-up timescale. As a corollary, these findings imply that throughout time persistent active basal foodwebs must have been present, sustaining the productivity of these higher trophic levels. The questions then naturally arise as to what extent evolutionary history has been preserved in the modern microbial biota in Antarctica, and to what extent microbial biodiversity shows the same degree of geographical differentiation as Antarctic metazoa.

Providing answers to these questions also has a broader relevance to understanding the rates and nature of diversification and adaptation of microbes. In particular, they have the potential to contribute to the long-standing debate as to whether microbes have a biogeography similar to macroscopic organisms. Indeed, as early as the 19th century, Darwin and de Candolle had observed that small organisms generally have larger distributional ranges than larger species. This idea was further developed by the Dutch microbiologist Baas-Becking (1934) in his famous dictum: “everything is everywhere but the environment selects” and more recently, by Fenchel and Finlay (Fenchel 1993; Finlay et al. 1996; Finlay 2002) in the so-called Ubiquity hypothesis. Fundamental to this hypothesis is the idea that the enormous population sizes of microbes combined with an easy dispersal lead to low global diversity of microorganisms and geographical distributions that are only constrained by the

availability of suitable habitats. As a consequence, most microbial species should therefore be virtually cosmopolitan.

Here we summarize results from our recent work within the framework of the Belgian projects HOLANT and AMBIO (both contributing to SCAR EBA Work Package 1: Evolutionary history of Antarctic organisms). We show that, based upon different independent approaches, clear biogeographical patterns are emerging for some groups of phototrophic microbes, and hypothesize that these are to a large extent the result of geographical isolation. These examples also serve as a framework to discuss a number of general issues related to microbial biodiversity and biogeography in Antarctica.

Strong latitudinal gradients in taxonomic richness and turnover rates of diatoms

One prediction of the ubiquity hypothesis is that, as a result of global dispersal, latitudinal gradients in diversity should be weak or absent once ecological controls are factored out (Hillebrand & Azovsky 2001, Finlay & Fenchel 2004). Demonstrating large-scale trends in microbial diversity is not as straightforward as it might seem. Studies of large-scale trends in local and regional diversity of microbes have been hampered by uneven and/or incomplete sampling over large geographical scales (in Antarctica this also holds for metazoa, see Adams et al. 2006, Chown & Convey 2007), by the lack of standardization in the delineation of taxonomical units on the basis of morphological criteria, and more recently, also in the molecular markers used to delimit OTUs (operational taxonomic units) and the techniques used to produce inventories of genetic diversity for single samples.

In a recent study, a large global dataset consisting of diatom inventories of nearly 2000 lakes and pools was used to investigate latitudinal trends in diversity (Vyverman et al. 2007). This dataset was assembled by merging several regional datasets used in paleolimnological studies. Although the overall sampling methodology and the analytical protocols for diatom enumeration were comparable in all studied regions, it was not possible to merge species lists because of nomenclatural problems and inconsistencies and, in particular because of differences in species concepts and cryptic diversity (Vyverman et al. l.c.). These problems were alleviated by investigating diversity patterns at the genus level. As in many groups of organisms,

genus richness is a power function of species richness, which indicates that any trends observed at the genus level should also reflect similar trends at the species level. Grouping the lakes into equal-sized grid cells of 10 000 km^2 and extensive resampling was applied to account for differences in sampling effort in different geographic regions, and to calculate mean local richness (the average number of genera occurring in lakes in a grid cell) and mean regional richness (the total number of genera present in a grid cell).

The results of this analysis were strikingly different from the predictions based on the ubiquity hypothesis. Both local and regional diversity showed strongly asymmetric latitudinal gradients (Fig 1). In the Southern Hemisphere, local and regional richness declined in a linear fashion with increasing latitude. In contrast, in the Northern Hemisphere, the gradient between local richness and latitude was hump-shaped between 55° and 70°N, while the gradient between re gional richness and latitude was virtually flat. Limnological conditions that are known to strongly influence diatom community structure however were not significantly different between Northern and Southern Hemisphere lake districts. In contrast, the degree of geographical isolation and connectivity between lakes were good predictors of regional and local diatom diversity, respectively. Furthermore, these results are consistent with the inverse relationship between taxonomic turnover rates and connectivity observed in the same data set (Verleyen et al. 2009). This does not mean that ecological factors do not play a role in structuring diatom communities, but rather that ecological constraints play a minor role in comparison to dispersal limitation with increasing geographical extent.

Indications of endemism and bioregionalization of diatom floras

If our assertion is correct; that dispersal constraints - resulting from either pure geographical isolation or from geographical variation in propagule flux associated with migrating birds and animals or with atmospheric circulation patterns- influence global patterns in regional and local diatom diversity, it can be expected that Antarctic and Sub-Antarctic diatom floras would be characterized by a high degree of endemism.

Several fine-grained taxonomic revisions of regional diatom floras suggest that in some areas within Antarctica at least 40 per cent of the species are endemics

(Schmidt et al. 1990; Sabbe et al. 2003; Van de Vijver et al. 2005; Spaulding et al. in press). Extending these studies, we have established a fully revised and intercalibrated database of diatom inventories of nearly 500 lakes covering most of the Antarctic and sub-Antarctic (Van de Vijver, unpubl., Verleyen et al. unpubl.). Preliminary analyses of this data set confirm that the diatom floras of Sub-Antarctic and Antarctic regions are significantly less diverse in their diatom floras than (Sub)Arctic floras, and that they show a high degree of endemism (Plate 1), with species varying in their geographical ranges. Furthermore, different biogeographical provinces can be identified that correspond to major boundaries in the distribution of invertebrate faunas and higher plants, indicating that the large-scale and long-term controls of the biogeography of macroorganisms and microbes must be similar.

While a robust time-calibrated phylogeny for the diversification within major clades of diatoms is not yet available, fossil evidence may shed light on the changes that have occurred during the past millions of years and provide evidence of the persistence of genera and species. The few studies available to date suggest that there is great potential for detailed studies of geological deposits to understand the evolution of diatom floras in Antarctica. In the Marine Isotope Stage 5e (the last interglacial period, spanning about 130-117,000 years ago) sediments of proglacial Progress Lake in the Larsemann Hills (Hodgson et al. 2006) several diatom species were found that are today absent from the Antarctic continent but occur on several sub-Antarctic islands. This indicates that species' ranges are dynamic over longer time scales and may change in response to a combination of changing climate dynamics, atmospheric circulation patterns and ability to disperse and colonise new environments; similar to the latitudinal shifts observed in terrestrial vegetation in the Northern Hemisphere during successive glacial cycles. Alternatively, these diatoms may have been present in Antarctica until they were finally driven to extinction during the last glaciation. In a recent study, Lewis et al. (2008) described a well-preserved sequence of fossil diatoms from a moraine-dammed basin in the western Olympus Range in the Mc Murdo Dry Valleys sector. The assemblages that were living in the lake around 14 million years ago were very different at the genus level from modern diatom communities in Antarctic lakes and bear a high resemblance to low-ionic strength lakes of the Arctic. Studies of these assemblages at the species level would provide evidence of their similarities to modern Arctic and/or Antarctic floras and inform us about their rates of change and divergence.

Evidence for long evolutionary histories of green algae

In diatoms, the elaborate structure of the siliceous cell walls offers a wealth of information that is used to delineate species. Repeatedly, studies combining morphological and molecular-genetic approaches with experimental breeding studies have demonstrated a good agreement between morphological, molecular and reproductive data (e.g. Behnke et al. 2004, Casteleyn et al. 2008, 2009, Vanormelingen et al. 2007,). In green algae, however, delimitation of species and higher taxa based on morphology is contentious, especially in groups that are morphologically conservative and exhibit convergent evolution towards reduced morphology (e.g. Huss et al. 1999). For Antarctica, most data on green algae are largely restricted to morphology-based taxonomic inventories (Broady 1996, Cavacini 2001, Mataloni & Pose 2001, Adams et al. 2006, Fermani et al. 2007; Zidarova 2007) and suggest a high degree of cosmopolitanism. The currently available molecular data are fragmentary, and consist of a number of isolated taxonomic and ecophysiological studies on individual taxa (e.g. Moro et al. 2002; Pocock et al. 2004; Fell et al. 2006).

However, in a recent study (De Wever et al. 2009), molecular phylogenetic techniques, including molecular clock analysis of nuclear encoded 18S rRNA gene sequences were used to characterize 61 Antarctic microchlorophyte isolates from 13 maritime and 30 continental Antarctic samples. Phylogenetic analysis showed that 14 distinct freshwater taxa were distributed among the classes Chlorophyceae and Trebouxiophyceae. Apart from one strain, all Antarctic sequences were different from non-Antarctic sequences currently available in GenBank. Although there is no generally-accepted threshold of 18S rRNA sequence divergence for defining green algal taxa, most Antarctic sequences are divergent enough to be considered distinct species, genera or even higher-order taxa. These results thus indicate a wide phylogenetic diversity of apparently endemic Antarctic lineages at different taxonomic levels. They further contrast with earlier morphological studies and support the notion that Antarctica has developed a distinct regional flora rather than being dominated by cosmopolitan taxa. Consequently, given the high morphological similarity between unrelated microchlorophyte species that has resulted from convergent evolution, future studies should use molecular data, in addition to morphological data, to study green algal biodiversity and biogeography in Antarctica (Plate 2).

Estimated ages of the Antarctic green algal lineages based on a time-calibrated phylogeny ranged from 2.7–9.9 Ma for a number of chlamydomonad isolates (Chlorophyceae) to over 17–84 Ma for the majority of the sequences and 330–708 Ma for a trebouxiophycean isolate SC2-2. The widely differing branch lengths of the Antarctic lineages point to several independent but rare colonization events over a long time frame, and long-term survival in glacial refugia. As the phylogenetic tree was calibrated at only a single node (Chlorophyta– Streptophyta split between 700 and 1500 Ma) and relied on sequence data that were available on GenBank, the divergence times of the different Antarctic microchlorophyte strains should be regarded as rough estimates. The majority of the lineages (16 out of 26) have estimated ages between 17 and 84 Ma and probably diverged from their closest relatives around the time of the opening of Drake Passage (30–45 Ma) during the Eocene, which initiated the first transient glaciations on the continent. The lineages with longer branch lengths, including SC2-2 (330–708 Ma), have estimated ages that precede the break-up of Gondwana (65–100 Ma). Together, these findings suggest the existence of refugia being present during successive glacial cycles (Convey & Stevens 2007; Convey et al. 2008, 2009) and conflict with the recolonization hypothesis, which proposes that fast colonization rates have resulted in the dominance of cosmopolitan species on Antarctica.

Our data also shed light on green algal dispersal within the Antarctic continent. The majority of Antarctic taxa were detected in only one Antarctic region, while none of the taxa was found in more than three of the five regions sampled. This implies that dispersal rates within Antarctica could be low and/or that immigrants are competitively excluded as a result of priority effects. Only two taxa, belonging to the genera *Chlorella* and *Scenedesmus*, were detected in three of the five regions, suggesting that these taxa may have more easily dispersed over the Antarctic continent. This is in agreement with Lawley et al. (2004), who found a similar lack of overlap between the eukaryotic biota of ‘patterned ground soils’ using a clone library approach from several widely separated Antarctic locations, with only a few taxonomic units showing apparently wider distributions. However, we have to bear in mind that these results were obtained from a small number of sampling sites that may differ in limnological properties. Extended taxon sampling and the use more variable molecular markers (such as rDNA internally transcribed spacer - ITS) will

thus be required to elucidate phylogeographic patterns of green algal taxa within Antarctica.

Hidden diversity and endemism in cyanobacteria

Cyanobacteria are a particularly successful group in Polar Regions. They are abundant in lakes and ponds where they form benthic microbial mats, but also occur in the water column as well as in soils, cryoconite holes, and cryptoendolithic habitats (Vincent, 2000). Although several studies indicate the existence of genotypes found only in Antarctica (e.g. Priscu et al., 1998; Bowman et al., 2000; Smith et al., 2000; Vincent et al., 2000; Nadeau et al., 2001; Christner et al., 2003; De la Torre et al., 2003; Taton et al., 2003; Casamatta et al., 2005; Jungblut et al., 2005), comprehensive studies of the species diversity and geographical distribution are still in their infancy. As for green algae, molecular diversity of cyanobacteria is higher and therefore does not always coincide with the morphological diversity at ecological and biogeographical levels. Moreover, they are a very ancient group, responsible for the oxygenation of the Precambrian atmosphere, about 2.3 billion years ago. Recent and ongoing studies, based on combined morphological studies and sequencing of 16S and ITS rDNA of strains as well as studies of uncultured diversity using clone libraries, lend further support to the idea that also for cyanobacteria much of the diversity remains to be discovered and that this diversity includes many potentially endemic taxa in Antarctica (Taton et al. 2006, a, b) (Plate 2). However, these authors also found a number of OTUs containing non-polar sequences. Interestingly, these OTUs appear to be more widely distributed within Antarctica, which would support the idea that cosmopolitan OTUs are well adapted to transport and colonization and thus were quite successful in their dispersal and occupation of new habitats in different regions of Antarctica. Furthermore, OTU's based on molecular markers such as the 16S rRNA gene or ITS sequences might encompass significant microdiversity as suggested by slight variation in the sequence data. Such microheterogeneities might correspond to different ecotypes (Fuhrman and Campbell 1998), and may further increase the genotypic diversity.

Diversity of bacteria

In parallel to the above-mentioned studies of other groups of micro-organisms, the isolation of heterotrophic bacteria from lacustrine and terrestrial habitats on a

selection of different media and their subsequent preliminary identification based on partial 16S rRNA gene sequences is revealing a large diversity and variation between sites. Furthermore, fingerprint profiles based on rep-PCR indicate that very few fingerprint types are recovered in more than one site (3.5%). Depending on the site, approximately 5 to 50% of the 16S rRNA gene sequences recovered display less than 97% sequence similarity to named entries in the EMBL database (Peeters et al., in preparation), indicating that they represent unrecorded taxa which are potentially new to science. Previous studies of Antarctic bacterial diversity have also reported significant numbers of new groups (Brambilla et al., 2001; Van Trappen et al., 2002) and in recent years many new species and genera have been described from Antarctica (for example, Mevs et al. 2000; Van Trappen et al. 2004a, 2004b, 2005; Hirsch et al., 2004; Yi et al., 2005; Lee at l., 2007). Most of these have not been reported from elsewhere and may be endemic to Antarctica. However, as bacterial diversity in general is estimated to be several orders of magnitude larger than the currently named species and genera (Hugenholtz et al., 1998; Schloss and Handelsman, 2004), it cannot be excluded that the taxa found in Antarctica may be found in other extreme cold habitats elsewhere on the planet. For example, *Shewanella hanedai* has been reported from the Arctic Ocean and from Ellis Fjord, Antarctica (Bowman et al., 1997); *Shewanella frigidimarina* was isolated from ice and cyanobacterial mats in Antarctica (Bowman et al., 1997) and also recovered from water in the Western Greenland Sea (Mergaert et al., 2001). Although information on the distribution of bacteria is fragmentary at present, as more habitats are studied and bacteria are identified to species level with molecular techniques, new information will allow more reliable conclusions on bacterial distribution and endemism.

Discussion

The assemblage of regional biota involves a balance between processes that operate over short time scales such as dispersal, colonization and extinction as a result of regional changes in geophysical and climatic conditions and biotic interactions, as well as, over longer time scales, migration of entire biota, speciation and extinction. For many groups of macroorganisms, decades of intensive recording

of species' distributions, evidence from the fossil record, phylogenetic studies and extensive sampling of regions worldwide; provide an extensive and solid framework to study the processes affecting the composition and spatial-temporal dynamics of regional floras and faunas. For microbes, in contrast, much basic research remains to be done on all of the above fronts. The enormous diversity of prokaryote and eukaryote microbes makes this a challenging undertaking for most major taxonomic groups.

Extrapolating from the evidence for a strong regionalization and endemism among Antarctic diatoms, green algae and cyanobacteria discussed above, we hypothesize that these are not exceptional cases among the Antarctic microbial flora and fauna. For ciliates, for example, several cases of morphospecies endemic to the Antarctic continent are already known (Petz et al. 2007). Out of a total of 334 species identified in both polar regions, only 44 species were common to both Arctic and Antarctic freshwater bodies. While many morphospecies were classified as cosmopolitans, over 20% of the taxa found in any one of the studied areas were new to science. The low similarity in species composition between both polar areas further suggests that long-distance dispersal of limnetic ciliates is restricted and that some species have a limited geographical distribution.

One of the major flaws of the ubiquity hypothesis is the uncritical application of a (wide) morphospecies concept to eukaryotic microbes. Although we do not intend to review the many fundamental/philosophical and practical issues related to the definition of species concepts, there is abundant evidence that for many if not most eukaryotic microbial groups, morphospecies contain much hidden diversity (e.g. Mann, 1999, Vanormelingen et al., 2008). In the case of diatoms, we are confident that the currently-adopted fine-grained morphospecies concept better reflects discontinuities in morphological variation and thus species' boundaries than the broad morphospecies concept used in earlier studies. Indeed, the use of a narrow morphospecies concept is broadly supported by several in-depth case studies on unrelated groups of diatoms which show good agreement between fine-grained morphological classification, molecular-genetic markers and breeding studies. The same problem was highlighted for cyanobacteria by Komarek (1999) who determined that about 60% of cyanobacterial morphospecies in ice-free areas of King George Island, were endemic. He explained the apparent cosmopolitanism of the

cyanobacterial diversity based on the morphology by the fact that previous authors used determination keys written for temperate regions without considering the different ecologies.

However, the use of molecular data to define species is not without difficulties itself since marker choice and the level of sequence similarity used in the delimitation of OTUs or formal species will evidently influence conclusions as to whether endemism occurs within a given group. For example, Martiny et al. (2009) found that at the finest taxonomic level geographic structuring occurred within the cosmopolitan marine planktonic cyanobacterium *Prochlorococcus*, while in contrast, at a higher taxonomic level the distribution of phylotypes was correlated with environmental conditions. Rybalka et al. (2009) studied the genotypic diversity of the chloroplast-encoded *psbA/rbc*L spacer region within Antarctic Tribonemataceae and compared these to available sequence data from temperate and Arctic strains. Applying the monophyletic species concept, they did not find any evidence for the presence of endemic species. However, none of the Antarctic sequences were identical to sequences of temperate regions. This suggests that at the within-species level significant microdiversity exists that is geographically structured and that even when phylotypes appear to be cosmopolitan, this does not necessarily mean that Antarctic isolates/populations are identical to populations living at lower latitudes, nor that they are connected by current gene flow. In a study of the heterotrophic flagellate genus *Spumella*, Boenigk et al. (2006) found that only a minority of the morphotypes and (18S rRNA) phylotypes isolated from the Antarctic continent followed the worldwide trend of a linear correlation between ambient (air) temperature during strain isolation and heat tolerance of the isolates. A high percentage of the Antarctic isolates were obligate psychrophilic, while isolates from locations on all other continents tolerated higher water temperature, even if some of them were isolated at low ambient temperatures. This drastic deviation of Antarctic representatives of *Spumella* from the global trend of temperature adaptation of these organisms provides strong evidence for the existence of dispersal or colonisation barriers, a subtle form of endemism. It would be interesting to know if this ecophysiological differentiation is mirrored in geographical structuring of more variable molecular markers.

One of the mechanisms that could underlie these different degrees of geographical structuring of genetic and ecophysiological variation could be differences in dispersal ability. There should be no surprise to find that different groups of microbes differ in their dispersal ability and level of endemism given their widely divergent evolutionary ages and genome make-up. However, very little is known about microbial dispersal and colonization, which was aptly illustrated in a recent review of this topic by Pearce et al. (2009). For example, recent or continual colonization could explain the small proportion of endemic fungi in Antarctica and the numerous fungi that appear to have a bipolar distribution (e.g. Galloway & Aptroot, 1995; Vishniac & Onofri, 2003). Again, however, different molecular markers for fungi should be tested to assess whether these indeed represent globally dispersed organisms or geographically isolated populations that have diverged allopatrically.

Whereas for eukaryotic microbes, overall diversity within Antarctica appears to be moderate, making it feasible to undertake comprehensive large-scale inventories to obtain a robust view of biogeographical patterns, the huge diversity of prokaryotes makes such analyses much more problematic. In Antarctica, recent studies of bacterial 16S rRNA gene clone libraries and community fingerprinting have discovered that prokaryotic communities are highly diverse, even in the extreme terrestrial systems in the ice-free oases (e.g. Niederberger et al. 2008, Verleyen et al, unpubl.). Culture-dependent approaches are revealing a high degree of new diversity, including numerous new species as well as higher taxa (for example, Mevs et al. 2000; Hirsch et al., 2004; Van Trappen et al. 2004a, 2004b, 2005; Yi et al., 2005; Lee at l., 2007). Rarefaction analyses based on clone library results further indicate that most microbial habitats and regions remain under-sampled. Yet, some evidence indicates that also for these organisms, biogeographical rules of macroorganisms may be applicable. Yergeau et al (2009) used PhyloChip analyses to study bacteria and archaea along a latitudinal gradient ranging from 51°S (Falkland Ils.) to 72°S (Coal Nunatak). Not only di d they observe a lower number of taxa detected in individual samples than typically reported for temperate soil environments, but the number of bacterial and archaeal taxa significantly decreased with increasing latitude, with a large reduction in the southernmost sites (Fossil Bluff and Coal Nunatak). This pattern agrees well with diversity estimates based on 16S

rRNA gene libraries (Yergeau et al., 2007). Interestingly, studies of northern hemisphere latitudinal gradients have not shown such latitudinal patterns in bacterial diversity, a situation that is similar to the patterns we described above for diatom diversity. A systematic examination of this pattern in other microbial groups (see also Hodgson et al., this volume) would be interesting and could reveal if these differences in latitudinal patterns of microbial diversity between the Southern and Northern Hemispheres can be generally applied.

Conclusion

Microbial biogeography in Antarctica offers many challenges and opportunities to study the nature and rates of adaptation of different groups of microbes to the harsh conditions and geographically isolated habitats on the continent and to investigate how much of the modern microbial diversity evolved *in situ* or is the result of more recent colonization events as the continent changed from a temperate forested state to the current ice-house conditions. High-throughput sequencing of DNA and RNA libraries now permit greatly increased sampling intensity for several phylogenetic groups, but also permit investigation of the geographical distribution of both taxa and functional genes present in microbial genomes. The ubiquity hypothesis has had an important impact on the discipline of microbial biogeography, and will remain to function as a null hypothesis against which to evaluate new data. Evidence is accumulating, however, that at least in Antarctica, the microbial biota is to a large extent the result of geographical isolation, and not just a subset of globally distributed taxa adapted to the extreme environments that characterize the continent.

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Figure captions

Figure 1: The interhemispheric asymmetry in mean local (a) and mean regional (b) lacustrine diatom richness showing that highly connected sites such as those in lake rich regions in the Northern hemisphere hold a significantly higher number of genera than Antarctic lakes and the isolated islands in the Southern Ocean. Lakes were grouped into equal sized grids of 100 by 100 km. For regional richness data, only grids containing more than 10 samples were included. Mean local richness between 70 and 40°S decreases linearly with latitude in the Southern Hemisphere ($y = 0.3394x + 30.502$, $R^2 = 0.3914$, $p<0.001$) while in the Northern Hemisphere it shows a hump-shaped relationship with latitude and peaks between 55 and 70°N ($y = -0.0134x^2 + 1.5866x - 24.489$, $R^2 = 0.194$, all constants significant at $p<0.05$). Mean Regional richness strongly declines with latitude in the Southern Hemisphere ($y = 0.8823x + 75.228$, $R^2 = 0.695$, $p<0.001$), whereas it is virtually flat in the Northern Hemisphere and no significant regression line can be calculated. Modified from Vyverman et al. (2007).

Plate 1. Endemic diatom taxa from the Sub-Antarctic Region (SA), the Maritime Antarctic Region (MA) and the Antarctic Continent (CA). SA: Figs 1-2. *Psammothidium incognitum* (Krasske) Van de Vijver, Figs 3-4. *Psammothidium manguinii* (Germain) Van de Vijver, Fig. 5. *Diadesmis ingeae* Van de Vijver, Fig. 6. *Diadesmis crozetikerguelensis* Le Cohu & Van de Vijver, Fig. 7. *Staurosira jolinae* Van de Vijver, Fig. 8. *Adlafia bryophiloides* (Manguin) Van de Vijver, Fig. 9. *Frustulia pulchra* Manguin. MA: Fig. 10. *Luticola muticopsis* (Van Heurck) Mann, Fig. 11. *Luticola austroatlantica* Van de Vijver & Kopalová, Fig. 12. *Muelleria regigeorgiensis* Van de Vijver & Spaulding, *Stauroneis latistauros* Van de Vijver & Lange-Bertalot. CA: Fig. 14. *Muelleria peraustralis* (West & West) Spaulding & Stoermer, Fig. 15.

751 *Luticola murrayi* (West & West- Mann, Fig. 16. *Luticola gaussii* (Heiden) Mann. Scale bar
752 represents 10 µm.

753 Plate 2: Antarctic cyanobacteria (1-4) and green algal (5-9) taxa. Fig. 1: *Plectolyngbya*
754 *hodgsonii*, an Antarctic endemic representative. Fig. 2: *Calothrix* S16. Fig. 3: *Phormidium*
755 *pristleyi* S26. Fig. 4: *Nostoc* S50. Fig. 5-9: Green algal strains, respectively VI8, VPL9-5, I6,
756 WO8L-2 (*Scenedesmus* sp.) and EO5-4 (*Chlorella* sp.).Scale bars represent 10 µm.
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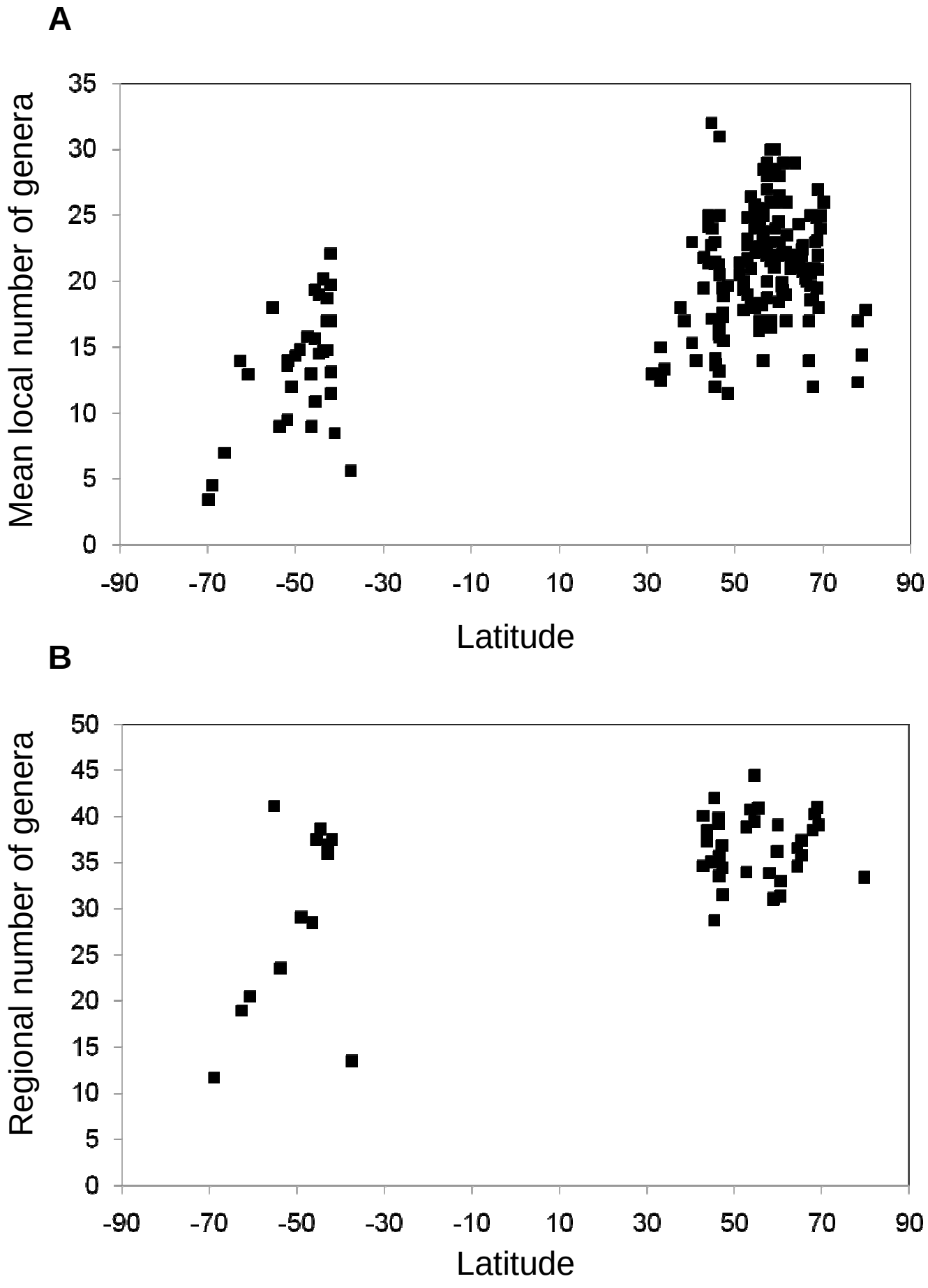
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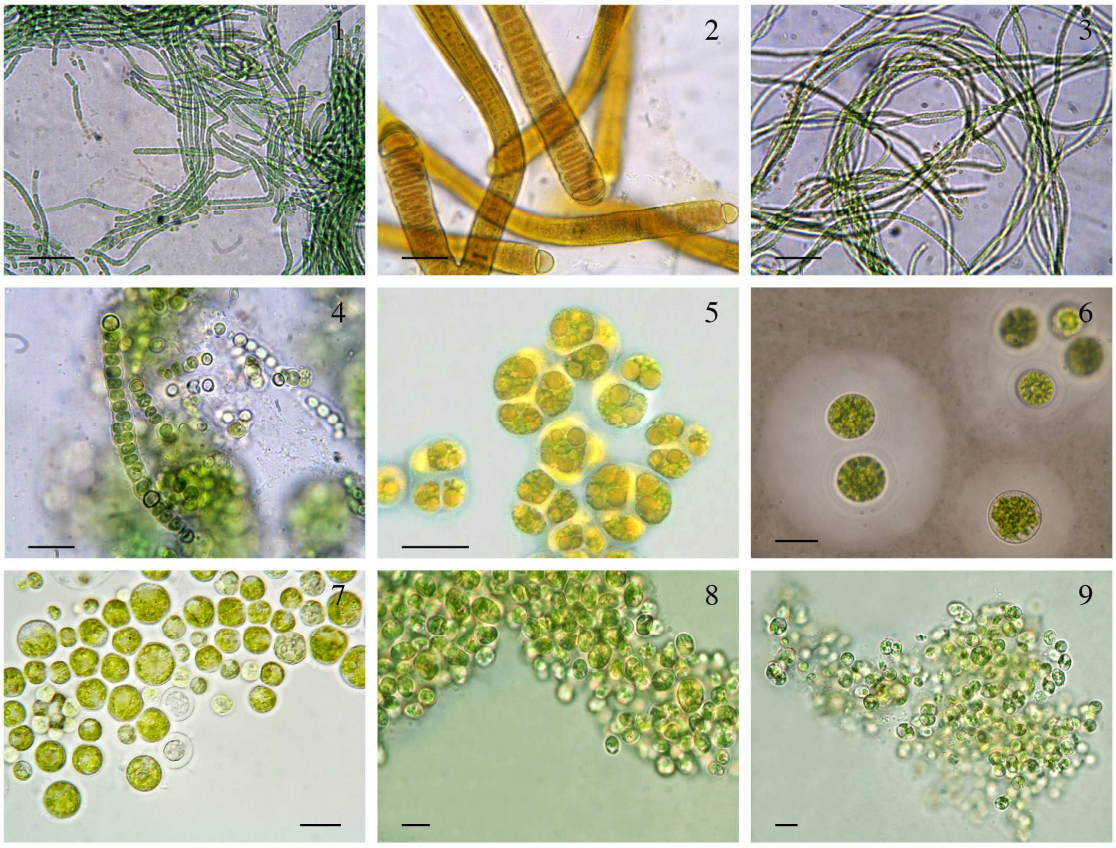

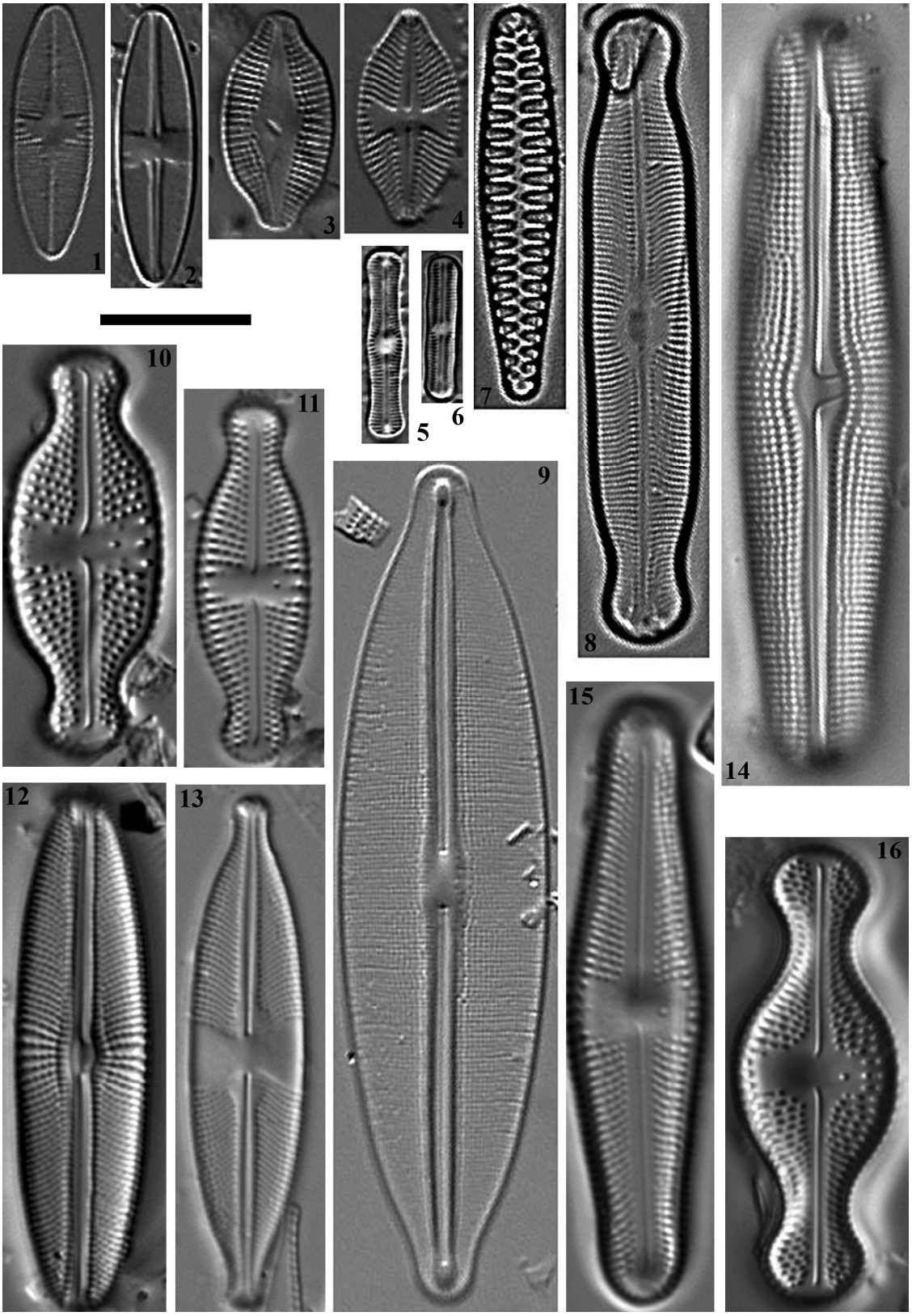
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